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The mature larva and pupa of *Semanga superba* (Lepidoptera: Lycaenidae)

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Abstract: The final instar larva and pupa of *Semanga superba deliciosa* Seitz [1926] from Peninsular Malaysia are described and figured. The highly myrmecophilous caterpillar is associated with a *Dolichoderus* species. The pupa is a probable mimic of bird droppings. Epidermal organs of caterpillar and pupa are figured. The pupa bears paired hemispherical organs on the eighth abdominal segment which are probably homologous to the larval tentacle organs. The presence of these pupal organs is suggested to be a synapomorphic character state of the subtribe Arhopaliti. The findings are compared with data on morphology and life-histories of related Oriental species.

Die Altraupe und Puppe von *Semanga superba* (Lepidoptera: Lycaenidae)

Zusammenfassung: Altraupe und Puppe von *Semanga superba deliciosa* Seitz [1926] aus Westmalaysia werden beschrieben und farbig abgebildet. Die Raupe frißt an Junglaub von *Saraca thaipingensis* (Caesalpiniaceae) und mindestens einer weiteren Familie von Holzgewächsen. Sie ist stark (möglicherweise obligat) myrmekophil und wird von Ameisen der Gattung *Dolichoderus* besucht. Die Ameisen nehmen nicht nur Sekrete des dorsalen Nektarorgans auf, sondern betrillern und belecken die gesamte Körperoberfläche. Die Raupe besitzt in großer Zahl kopfig verdickte, kurze Haare mit gezähnter Oberfläche wie auch typische dendritische Haare und Porenkuppelorgane. Alle diese Haare stehen wahrscheinlich im Zusammenhang mit der Myrmekophilie. Der Puppenhabitus deutet auf Vogelkotmimese. Die Puppen besitzen in identischer Position wie die larvalen Tentakelorgane ein Paar halbkugelige, mit winzigen Setae besetzte Strukturen, die vermutlich den Tentakelorganen homolog sind. Solche Organe sind auch von anderen Vertretern der Subtribus Arhopaliti bekannt und könnten eine Synapomorphie dieses Taxons darstellen.

Semanga Distant, 1884 (syn. *Keraunogramma* Röber, 1887) is a small Oriental genus of hairstreak butterflies in the subtribe Arhopaliti (Eliot 1973, 1992). The systematic position of the genus remains unresolved. Eliot placed it, together with the monotypic genus *Mota* de Nicéville,

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1890, in a separate "*Semanga* section" within the Arhopaliti. Characters of wing venation and male genitalia may indicate some relationship with the "*Surendra* section" (included genera following ELIOT (1973) and FIEDLER (1992 a): *Surendra* MOORE, 1879; *Zinaspa* DE NICÉVILLE, 1890; *Amblopala* LEECH, [1893]), yet the matter requires cladistic analysis of a broader data base. While the early stages of *Surendra* are quite well known (FIEDLER 1992a), the larvae or pupae of *Semanga* have apparently never been observed. We here describe and figure the mature larva and pupa of the Malayan subspecies *Semanga superba deliciosa* SEITZ, [1926]. Furthermore, we give a short account of our observations on larval biology.

Semanga superba (DRUCE, 1873) is widely distributed in the Oriental region from Thailand eastwards to Sumatra, Borneo (nominate subspecies) and the Sulu Archipelago (TAKANAMI 1988, SEKI et al. 1991). A close relative, *S. helena* (RÖBER, 1887), occurs on Sulawesi and surrounding smaller islands (TAKANAMI 1989).

Our observations were conducted in the vicinity of the Ulu Gombak Field Station of the Universiti Malaya, about 20 km northwest of the Malaysian capital Kuala Lumpur (Peninsular Malaysia; see MEDWAY 1972 for botanical information on the study area) and in the Bukit Renggit Wildlife Reserve, Pahang.

The mature larva

On 10. IV. 1993, one of us (P. S.) observed a prefinal (probably third) instar larva sitting on the underside of an older leaflet of the legume tree species *Saraca thaipingensis* CANTLEY ex PRAIN, 1897 (Caesalpiniaceae). The larva was taken into the laboratory and reared to the adult stage with cut young foliage of *S. thaipingensis*. All following descriptions are based on this individual.

The mature caterpillar (Fig. 4) reaches about 15 mm in length. It has the "onisciform" shape of most Lycaenidae caterpillars, quite flattened dorsoventrally, but not as flat as caterpillars of the genera *Arhopala* BOISDUVAL, 1832 or *Flos* DOHERTY, 1889. The ground colour is green. Prothoracic and anal plate are well developed, shiningly black in colour, and rather strongly sclerotized. The 3 thoracic segments and the abdominal segments A1–A6 each bear a pair of lateral cone-shaped projections (verrucae) furnished with a tuft of long, erect whitish setae. At the anal end, the cone-shaped paraprocts (cf. the configuration in *Hypolycaena*

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othona (HEWITSON, [1865]): FIEDLER 1992 b) likewise form verrucae and carry some long, erect setae. On the dorsum of the larva, long setae are absent. The spiracles are black.

There is a paramedian series of dark dorsal markings tapering from A1 to A6 and intermingled with a wavy yellowish and red line. The dorsum of the second thoracic and especially of the seventh abdominal segment are ivory-coloured to reddish brown. At the rear margin of the large marking on A7 there is a well developed dorsal nectar organ (see below). A pair of whitish eversible tentacle organs inserts in distinctly elevated, sclerotized black sheaths on the eighth abdominal segment (Figs. 4–6).

Microscopical examination of the mature caterpillar's exuvia mounted on a slide in Euparal revealed the following setal types:

1) Long, erect bristles. These occur on the lateral verrucae and paraprocts and are the only hairs visible on the macrophotographs (e.g., Fig. 4).

2) Medium-sized stout cone-shaped hairs inserted in large buttressed chalazae (Figs. 7–8; see BALLMER & PRATT 1988 for terminology). Their hair shafts are somewhat dentate and thickened distally. Such hairs occur dorsally in groups of 3–8 in paramedian position from the second thoracic to the sixth abdominal segment. 1–2 such hairs are situated near the lateral edge of the opening of the dorsal nectar organ (= DNO) on A7.

3) Filiform setae: on either side of the prothorax there is one filiform seta inserted at the posterio-lateral corner of the prothoracic shield.

4) Dendritic setae. There is a small group of ca. 6 dendritic setae at the posterior margin of the DNO.

5) Stout "capitate" setae with distally broadening spiculate hair-shafts (cf. BALLMER & PRATT 1988) of somewhat variable size and shape (Figs. 9–11) occur in large numbers all over the larval surface, especially concentrated just behind the prothoracic shield and around the DNO. Alike in the type 2 setae, their chalazae are distinctly buttressed.

6) Pore cupola organs (PCOs). These glandular hairs with a circular sieve-plate instead of a hair shaft (Fig. 12) occur scatteredly all over the caterpillar, with prominent accumulations dorsally on T2, laterally around the abdominal spiracles, and dorsally around the DNO on A7.

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The pupa

The pupa measures some 13 mm in length. It is attached to the substrate with a strong girdle as well as with a ventral field of cremastral hooks, which insert into a large silk pad spun by the prepupal larva (Figs. 2–3). The ground colour is white, with black dorsal markings on the prothorax and anterior part of the mesothorax. There is a pair of mediolateral, supraspiracular rows of smaller black dots from A1 to A8, and irregular dark spots occur in the midline of T3–A2 and on the wing cases. The spiracles are brownish. The pupal colour pattern suggests a mimic of bird-dropping, as in other Lycaenidae butterflies (e.g. the Palearctic *Satyrium pruni* (LINNAEUS, 1758) or the Oriental genus *Logania* DISTANT, 1884).

There is a well developed stridulatory organ between A5 and A6. The pupa lacks any longer setae. Around the spiracles there are large groups of pore cupola organs (Figs. 13–14). Otherwise pore cupolas occur scatteredly, and the whole pupa is densely studded with lenticles. In contrast to *Surendra* pupae, trumpet-shaped setae are absent in *Semanga superba*. There is also no discernible cuticular scar of the larval DNO.

The most remarkable pupal structure is a pair of small elevated subspiracular bulges laterally on A8. This structure is light brown in colour (Fig. 2). Microscopic examination of the macerated pupal cuticle revealed that this bulge carries densely packed lenticles (setae without a distinct shaft: Fig. 15).

Biological observations

We observed larvae of *Semanga superba* on two different hostplants. The single larva found at Ulu Gombak fed on *Saraca thaipingensis*. In Bukit Renggit (19. I. 1988), one of us (K. F.) found 2 larvae of *S. superba* on *S. thaipingensis* and on an undetermined neighbouring non-legume shrub. Therefore, the species is certainly not monophagous. Caterpillars only fed

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Colour Plate

Fig. 1: Freshly eclosed male of *Semanga superba deliciosa*. **Figs. 2 & 3:** Pupa of *S. superba*, dorsal and lateral view. **Fig. 4:** Mature larva of *S. superba*, dorsal view. Note the shiningly black prothoracic and anal shields and the tentacle organs in elevated sheaths. **Figs. 5 & 6:** *Dolichoderus* ants tending the mature *S. superba* caterpillar. The ants lick the whole surface of the caterpillar, with special emphasis towards the prothoracic and anal shields. (Photographs 1, 5 & 6: P. SEUFERT; 2–4: K. FIEDLER.)

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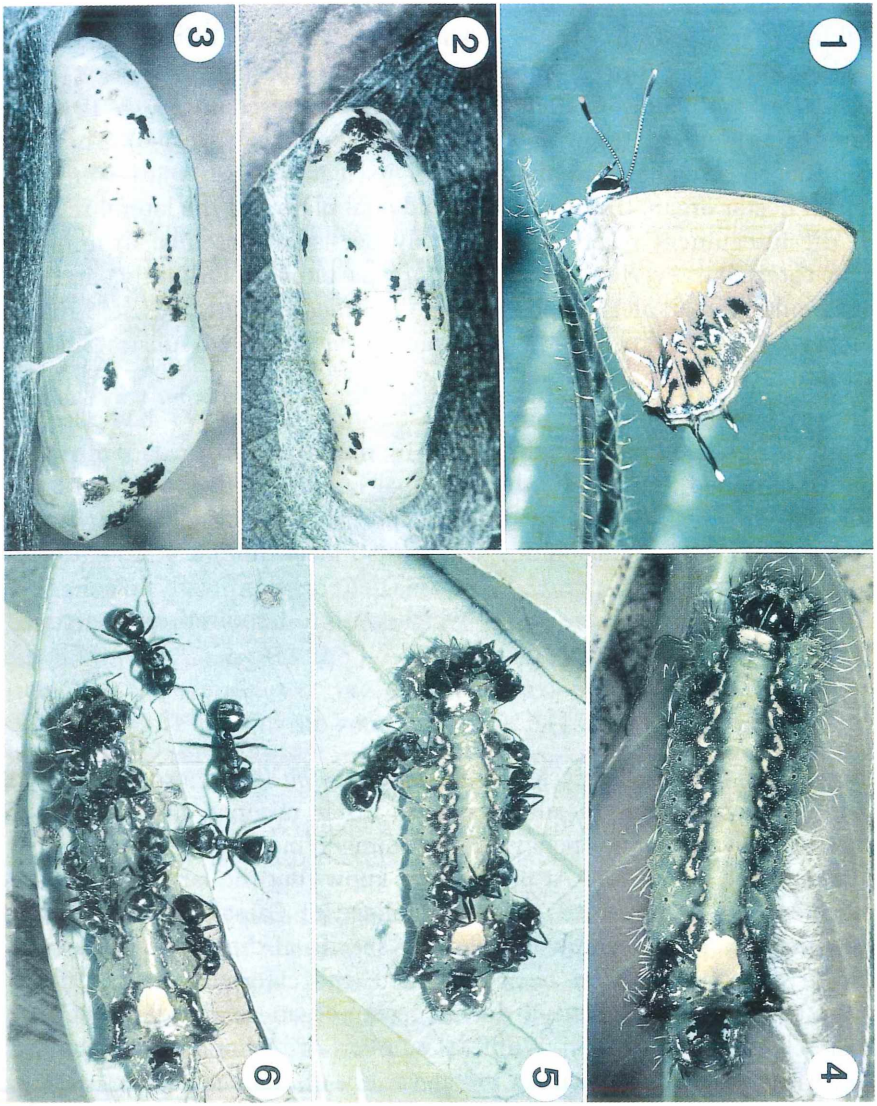

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on young, tender foliage of the hostplants. In captivity, the Ulu Gombak specimen fed inside a shelter of leaflets spun together with silk.

All larvae in Ulu Gombak and Bukit Renggit were intensively tended by large groups (> 30 worker ants per larva) of a *Dolichoderus* species (near *thoracicus,* subfamily Dolichoderinae). Even in captivity, 5-10 ants permanently associated with the mature caterpillar (Figs. 5-6). The ants continously accompanied the larva in its leaf shelter. Apart from the dorsal nectar organ, the prothoracic and anal plate and the lateral regions of the integument received particularly persistent antennal drumming. The caterpillar everted its tentacle organs almost constantly, and we often observed an alert response of the *Dolichoderus* ants ("excited runs": FIEDLER & MASCHWITZ 1988). Larva and pupa produced substrate-borne vibrations when molested.

The caterpillar found as prefinal instar on 10. IV. 1993 had already moulted into the final (fourth?) instar by the 16. IV. (exact date of moult not determined). On 21. IV. the prepupal larva settled down on a large silk pad, further fastened to the substrate by a strong girdle. Pupation occurred on 22. IV., and on 3. V. 1993 (8.50 local time) a male butterfly (Fig. 1) eclosed (pupal period 11 days). The teneral butterfly was densely covered with woolly loose scales, which were lost soon after emergence with the first flight activity.

Discussion

Most aspects of the life-cycle of *Semanga superba* (e.g. reproductive and oviposition behaviour of adults, precise instar number, morphology of eggs and young larvae, behaviour of younger instars, hostplant range) remain to be uncovered. At present, we know that the larvae are highly myrmecophilous and feed on young foliage of Caesalpiniaceae and at least one other plant family. In all other species of the Arhopaliti, whose life-histories have as yet been described, the caterpillars are likewise myrmecophilous and have a dorsal nectar organ as well as a pair of eversible tentacle organs. While a number of Arhopaliti species are facultatively associated with a broad variety of ant genera (e.g. certain *Arhopala* spp., *Surendra:* FIEDLER 1992 a & unpubl.), others have obligatory and species-specific symbiotic relationships with particular host ants (e.g. *Arhopala pseudocentaurus* (DOUBLEDAY, 1847) and related species with *Oecophylla smaragdina* (FABRICIUS, 1793): NORMAN 1949, ELIOT 1992; some *Arhopala* species feeding on myrmecophytic *Maca-*

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ranga trees [Euphorbiaceae] with members of the *Crematogaster borneensis* complex: MASCHWITZ et al. 1984). Thus, with respect to myrmecophily, *S. superba* well fits into the range known from the subtribe Arhopaliti. This is also true for the ability to produce substrate-borne vibrations and pupal stridulations (NORMAN 1949, HILL 1993), although the functional connection of this phenomenon with myrmecophily (DEVRIES 1990) still awaits experimental proof for Lycaenidae immatures.

The very close and persistent ant-association of *Semanga superba* immatures, and the correspondence of tending ants in two different habitats separated by a distance of some 100 km, may indicate that myrmecophily could be obligatory in this species. This might also be one reason why the two larvae sampled in Bukit Renggit later on died in captivity in the absence of their host ants, although fresh *Saraca* flushes were supplied. The thick cover of the teneral adult butterfly with loose hair-like scales may well be a protection against ant attacks during and after eclosion, as is known for other obligately myrmecophilous lycaenids (e.g. COTTRELL 1984, 1987).

The hostplant relationships of *Semanga superba* remind of those found in *Surendra* and *Amblopala* (*Surendra* section sensu FIEDLER 1992a). Alike *Surendra* and *Amblopala*, the larvae of *Semanga superba* feed on legume trees (Fabales). Species of the *Arhopala* section sensu ELIOT (1973), in contrast, utilize trees in the families Fagaceae (15 spp.), Euphorbiaceae (6 spp.), Myrtaceae (5 spp.), Combretaceae (5 spp.), Lythraceae (5 spp.), as well as members of at least 10 additional plant families (FIEDLER 1991 & unpubl.). Only the polyphagous, obligately myrmecophilous *Arhopala pseudocentaurus* has yet been reported to feed on Fabaceae trees.

The overall gestalt of the *S. superba* caterpillar and pupa broadly differs from what is known about the immatures of other taxa in the subtribe Arhopaliti. Larvae and pupae of *Arhopala* and *Flos* are much more flattened and smooth; they lack epidermal verrucae. Caterpillars of these two genera often feed concealed in leaf rolls (for exceptions see MASCHWITZ et al. 1984), where they also pupate. The shouldered, striped larvae of *Surendra* are perfect mimics of the pinnate leaves of their Mimosaceae hostplants, and pupae of this genus are of the usual stout lycaenid type (FIEDLER 1992 a). Non-cryptic colourful caterpillars with distinct epidermal verrucae, or bird-dropping mimics in the pupal stage, were previously unknown from the whole subtribe.

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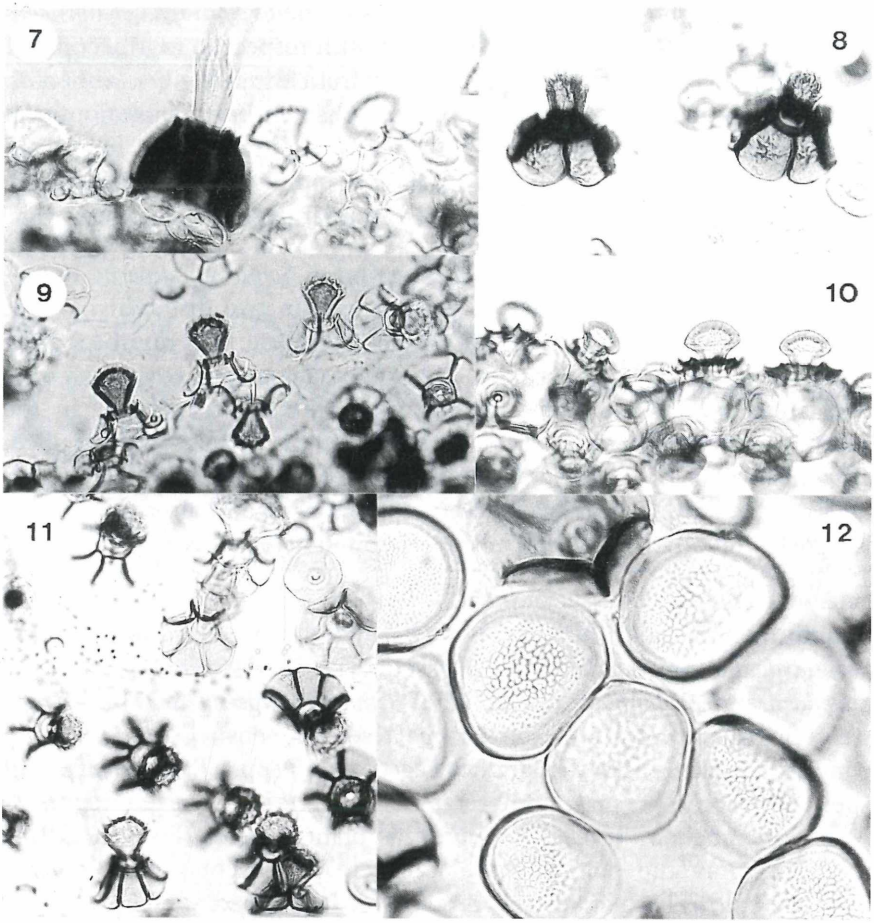

Figs. 7–12: Epidermal organs of the mature caterpillar of *S. superba*. **Figs. 7 & 8:** Dentate setae with buttressed chalazae. **Figs. 9–11:** Small capitate setae at various positions from the dorsal surface. **Fig. 12:** Group of pore cupola organs. (Photographs K. FIEDLER.)

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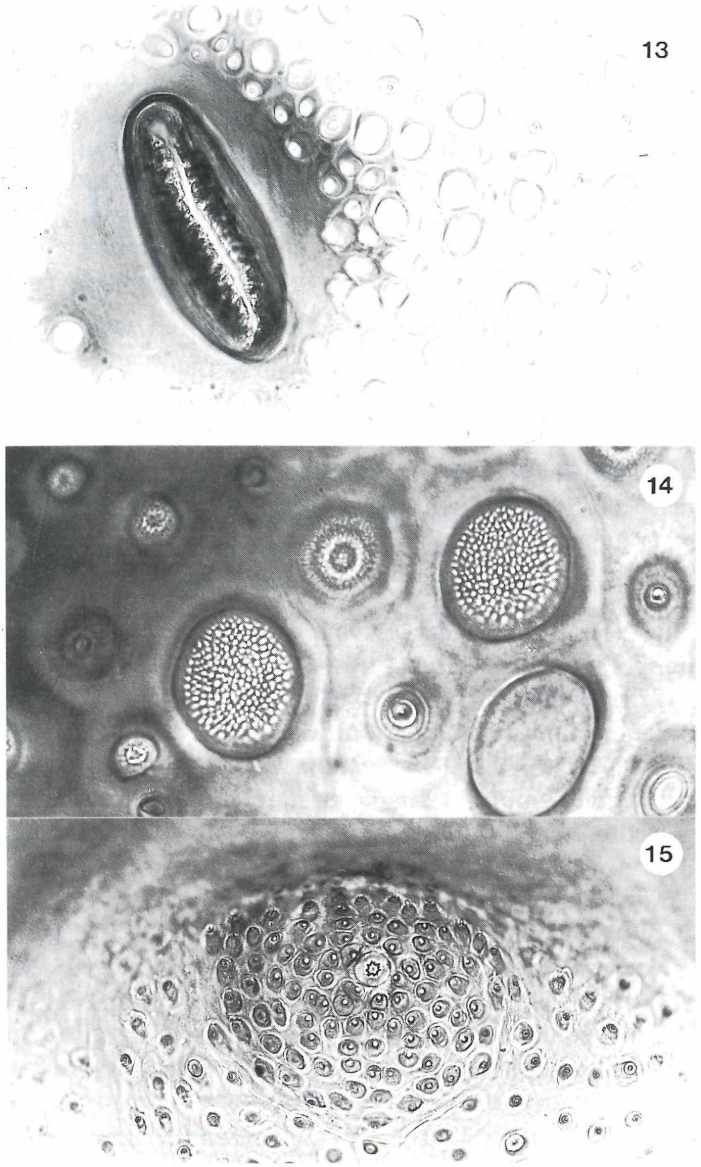

Figs. 13–15: Epidermal organs of the pupa of *S. superba*. **Fig. 13:** Abdominal spiracle with cluster of pore cupola organs and lenticles. **Fig. 14:** Close-up of two pore cupola organs (with sieve-plate) and one lenticle (without sieve-plate). **Fig. 15:** Hemispherical "bulge" organ on the eighth abdominal segment, probably homologous to the larval tentacle organ. (Photographs K. FIEDLER.)

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Microscopic examinations of epidermal organs, however, revealed close parallels to other Arhopaliti. The pupa of *Semanga superba* has a pair of peculiar epidermal bulges on A8 at the location of the larval tentacle organs. In exactly the same position, *Surendra* pupae possess a pair of hemispherical bulges covered with minute erect setae. Pupae of various *Arhopala* species possess an elevated hemispherical cluster of pore cupola organs in the same position (HILL 1993, FIEDLER, unpubl.). Whether or not all these structures are homologous to the larval tentacle organs, the striking concordance in location strongly suggests that they constitute a synapomorphy of the Arhopaliti.

Like the larvae of *Surendra florimel* DOHERTY, 1889 and some *Arhopala* species (FIEDLER 1992 a & unpubl.), the caterpillars of *Semanga superba* possess stout capitate setae in large numbers. They also have dendritic setae around the dorsal nectar organ. Since ants constantly lick the whole larval surface, where capitate setae are ubiquitous in *S. superba,* these hairs appear to be involved in myrmecophily, but their putative secretory nature awaits to be confirmed using histological techniques.

To sum up, despite some macroscopic divergence, our observations on the epidermal organs of immatures of *Semanga superba* corroborate ELIOT's (1973) assignment of this genus to the Arhopaliti. The phylogenetic relationships within that subtribe, however, cannot yet be resolved. While larval hostplant relationships (preference for Fabales, possibly a symplesiomorphic character state) connect *Semanga* with the *Surendra* section, the morphology of the pupal lateral organs suggests affinities with *Arhopala,* and in other respects *Semanga* has unique autapomorphic traits. A cladistic review of the Arhopaliti would be necessary to decide between these hypotheses. Data on the early stages of *Mota massyla* (HEWITSON, [1867]) (the closest relative of *Semanga* in ELIOT's classification), the genus *Zinaspa* DE NICÉVILLE, 1890, and on additional species of the genus *Arhopala* will also be helpful to elucidate the phylogeny and evolution of the Arhopaliti, the most speciose clade of all Oriental Lycaenidae butterflies.

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